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BIOLOGIC STUDIES IN THE SPHAERIALES—II ¹

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(WITH PLATES 35–38)

In Part I (18) of this investigation the writer has shown that many fungi now placed in the Sphaeriales have their asci borne in unilocular stromata. This type of development is found in the Dothideales. When these fungi are taken out, the order Sphaeriales will be characterized by the possession of a definite type of perithecium. This fructification will be defined as a globose to flask-shaped conceptacle, which arises from an archicarp, and opens by an ostium that is formed by the upward growth of the wall. Inside of the mature perithecium are to be found asci and paraphyses lining the base and sides and paraphyses lining the ostium. Stroma is always found on the outside of the perithecial wall. The presence of this stroma and the ostiolar characters will serve to distinguish this order from the Laboulbeniales and the Erysiphaceae.

The question arises as to how this order should be divided into families which will bring together related forms. The arrangement of the species in an ideal system of classification would

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certainly be based on natural relationships. The members of such a system would constitute an evolutionary series, beginning with the most primitive, and ending with the most highly specialized. In order to determine whether or not the species one groups together are phylogenetically connected, their life histories should be studied. Such investigations should serve as the basis for all taxonomic work.

Relationships in the Sphaeriales should be established on such important characters as the manner of development of the perithecium, types of asci and ascospores, and paraphyses and conidial characters. Such characters as the amount of stroma present, and the depth to which the perithecium or stroma is sunken in the substratum, are apparently most easily influenced by the environment, and so should not be used for major separations.

The object of this investigation is to show that the species with continuous dark-colored spores constitute a closely related group, all the members of which should be in the Xylariaceae, and further to determine the generic separations in that family. The common forms in this series are now placed in the genera *Sordaria*, *Melanospora*, *Rosellinia*, *Anthostomella*, *Anthostoma*, and the genera of the present family Xylariaceae. The writer will discuss these genera and will give the results of developmental studies in *Rosellinia*, *Hypoxylon*, *Ustulina*, *Nummularia*, and *Daldinia*.

Saccardo (24) placed these fungi in one group, the Phaeosporae, and based this entirely on the characters of the ascospores. In Lindau's (16) system of classification the family separations in the Sphaeriales are based on stromal characters, depth to which the perithecium or stroma is sunken in the substratum, the presence or absence of paraphyses, and the type of conidial fructification.

Sordaria in the Sordariaceae, *Rosellinia* in the Sphaeriaceae, and *Melanospora* in the Hypocreales, all have the same general perithecial characters, yet Lindau places them in widely separated groups along with other fungi which have entirely different types of asci, ascospores and paraphyses. Also *Anthostomella* is placed in the Clypeosphaeriaceae, and *Anthostoma* in the Valsaceae, and

the single difference between those genera is that the perithecia are single in *Anthostomella* and aggregated in *Anthostoma*. The members of the Xylariaceae, as understood by Lindau, represent the well-developed stromatic forms in the dark-spored series and constitute a related group.

HYPOXYLON Fries

Historical Sketch of the Genus

This generic name was created in 1791 by Bulliard (2), and the genus was placed in his first order of fungi which he separates on the basis of the internal origin of the spores. In this order are found what are now considered Myxomycetes, Fungi Imperfecti and Gasteromycetes as well as some Sphaeriales. Bulliard published sixteen species under the name of *Hypoxylon*, eleven of which are not *Hypoxylon* species in the present sense. According to the American Code of Nomenclature the first species described should be the type of the genus, and as this is *H. sphinctricum* Bull., a form which is not a *Hypoxylon*, this would change the generic concept that has been generally accepted. The International Code would not take this work as the beginning point, but would start with the "Systema Mycologicum" of Fries (7).

Persoon in 1801 (22: 8), in his genus *Sphaeria*, sec. II, Periphericae, published what are now considered as *Hypoxylon*, numbers 11-19 and 30 and 32-35. The number 11 here is *Sphaeria concentrica* (*Daldinia concentrica* (Bolt.) Ces. & De-Not.). The other numbers are *Hypoxylon* and *Nummularia*. Between numbers 19 and 30 are placed chiefly *Hypocrea* species.

In 1822 Schweinitz (25: 28-48) continued Persoon's conception of the genus *Sphaeria*. In his second subgenus, Periphericae, numbers 12-20 are *Hypoxylon*; in his third subgenus, Compressae, numbers 27, 29, 36, 38, 39 and 42-46 are *Hypoxylon*; in his subgenus Monostichae 81, 82 and 87 are *Hypoxylon*; and in his seventh subgenus, Caespitosae, number 122 is a *Hypoxylon*. The intervening ones in these groups are now considered as *Hypocrea*, *Diatrype*, and other genera of the Sphaeriales. The first published, number 12, is *Sphaeria concentrica*.

Fries (7: 319-359), in "Systema Mycologicum" in 1823, also

continued the genus *Sphaeria*. Here species of *Hypoxylon* are mixed with other fungi. In tribe III, Pulvinatae, the first species is *Sphaeria globosa*, now *Xylaria globosa*, and the second is *Sphaeria concentrica*, the other six being *Hypoxylon*. In tribe IV, Connatae, ser. I, are to be found only species of *Hypocrea*, while in ser. II there are 13 species of *Hypoxylon*. Tribe V, Glebosae, contains 8 species of *Hypoxylon*. Tribe VI, Lignosae, contains 5 species of *Hypoxylon* mixed with species of *Diatrype*.

In 1849 Fries (8: 383) in his "Summa Vegetabilium Scandinaviae" recreated the genus *Hypoxylon* for the first time since the work of Bulliard from tribes of his former genus *Sphaeria*. He gives Bulliard credit for this generic name. Here the genus is divided into Glebosae, Pulvinatae, Effusae, and Connatae. In the first subgenus he places first *H. ustulatum* Bull. (*Ustulina vulgaris* Tull.), following this with species now considered *Nummularia*. In the Pulvinatae are *H. concentricum* and pulvinate species of *Hypoxylon*; and in the last groups, Effusae and Connatae, are found effused forms of *Hypoxylon*.

According to the International Code all members of the Sphaeriales start with "Systema Mycologicum" of Fries, but as he contained these fungi within the larger group, *Sphaeria*, the genus did not have its beginning in that work. Bulliard cannot be given credit for this, because he was previous to Fries, and also our present concept of the genus *Hypoxylon* could not possibly evolve from his generic description nor from the species he described. Therefore, Fries in 1849 in "Summa Vegetabilium Scandinaviae" creates the genus *Hypoxylon*.

What should be considered the type of the genus? Neither Fries nor Bulliard designated a type species. The fact that Fries gave Bulliard credit for the genus and then transferred five of the Bulliard species apparently indicates that he considered these species as typical of the genus. These species are 1. *H. ustulatum*, 7. *H. nummularium*, 11. *H. coccineum*, 13. *H. granulosum* (*H. multifforme* Fries) and 16. *H. glomeratum* (*H. fuscum* Fries). If one agrees with Tulasne (30) in raising *H. ustulatum* and *H. nummularium* to generic rank, then *H. coccineum* would probably be considered the type of the genus. Shear (27: 84) considers this species the type. The writer does

not agree with the change made by Tulasne and thinks it sufficient to designate the five species transferred from Bulliard's genus as typical of *Hypoxylon*.

The following description of the genus is given in order to more clearly define its limits and to incorporate data brought out in this investigation.

HYPOXYLON Fries, *emend.*

Stroma globose to pulvinate to effused, erumpent, fleshy when young, leathery, woody or carbonaceous when mature. Perithecia several to many in stromata; paraphyses numerous, thread-like; asci cylindrical, arranged on sides and bottom of perithecia; ascospores brown to black, with an elongate hyaline depression, and uniseriate in the ascus.

Conidial layer formed first on an exposed ectostroma, later developing on old stromata in favorable weather. Conidiophores branched, hyphomycetous, hyaline to greenish-brown; conidia minute, borne apically, one to many, becoming lateral by the sympodial growth of the hypha.

Genera Split Off from the Genus *Hypoxylon*

1. *Ustulina* Tul. Tulasne (30: 23) in 1863 established this genus on *Hypoxylon ustulatum* Fries (1849), which was *Sphaeria deusta* in Fries's "Systema Mycologicum" (1823). This should have been *Ustulina deusta* (Fries), instead of *Ustulina vulgaris* Tul.

The separation is based on the character of the conidial stroma. Tulasne understood this to be more thick, fleshy, and superficial than in the other *Hypoxylon* species. In this respect Nitschke (19) agrees with him. Nitschke (19: 3), under "conspectus generum, b. stromate hypoxyleo," separates these genera as follows: "*Ustulina*, . . . stroma repando-pulvinatum. *Hypoxylon* . . . stroma subglobosum v effusum." The writer does not consider this a separation as many species of *Hypoxylon* are "repando-pulvinatum." Nitschke (19: 21) says this single species of this genus was correctly separated from *Hypoxylon*, since it agrees much more with *Xylaria* in its unmistakably peculiar habit in the consistency of the conidial-forming hymenium.

2. *Nummularia* Tul. In the above work Tulasne (30: 42)

created this genus on *Hypoxylon nummularium* Fries, *Sphaeria discreta* Schw., and a new form, *Nummularia dryophila* Tul. This separation is based on the supposed discovery of a conidial layer being borne under the stroma. He says at maturity it becomes erumpent and then produces the same appearance as in other species of *Hypoxylon*. Tulasne (30: Tab. V, figs. 11-19) illustrates the development of *N. Bulliardii* Tul. The drawing shows short conidiophores, bearing globose conidia, under a definite pseudo-parenchymatous stroma. Nitschke (19: 3) separates this genus as follows: "II. Conidia sub stromatis strato supremo nato, deinde libera," following Tulasne. In regard to the development (19: 56) he says he regrets that our knowledge of the conidial apparatus is limited to the discoveries made by Tulasne with *N. Bulliardii* and *N. discreta*.

3. *Daldinia* De-Not. *Sphaeria concentrica* Fries was the basis for this genus. De-Notaris (20) in 1863 observed that the concentric zonation of the stroma was more pronounced in this species than in the other species of *Hypoxylon*, and therefore erected the genus *Daldinia*. Neither Nitschke (19), Fries (8), nor Tulasne (30) had recognized this separation.

4. *Camarops* Karsten. The type of this genus is *C. hypoxyloides* Karst., described by him (15: 53) in 1873. According to von Höhnelt (14: 1218), this is the same as *Nummularia lutea* (Alb. & Schw.) Nits., or *Sphaeria lutea* Fries in "Systema Mycologicum," or *Hypoxylon luteum* Fries in "Summ. Veg. Scand." Also he says *Bolinia tubulina* (Alb. & Schw.), used as a subgenus under *Hypoxylon* by Nitschke (19), is in the same category. *Solenoplea microspora* Starback, according to von Höhnelt, also belongs here. The name *Bolinia* was first raised to generic rank in 1882 by Saccardo (24), while the name *Camarops* was created by Karsten in 1873. *Solenoplea* was described by Starback in 1902. Theissen (29) recognized that these three genera were identical.

This group is distinct from *Hypoxylon* on perithecial characters. *Camarops hypoxyloides* contains very long cylindrical perithecia which are closely appressed in a black stroma.

Development in the Genus *Hypoxylon*

The manner in which the stroma and perithecium arise in *Hypoxylon Howeianum* Peck has already been described by the

writer (18). *H. coccineum* Bull., which resembles the former closely, was studied by Lupo (17). The latter found three types of hyphae in the stroma from the time of its emergence from the substratum: "those that form the major part of the stroma, those that form the perithecium and Woronin hyphae, and those that form the superficial layers and probably conidiophores." (PLATE 36, FIG. 2.) The first type of hyphae comprise the entostroma, the second type the ones that arise from the initial coil or archicarp, and the third make up the ectostroma which is pushed up by the developing entostroma. Lupo says further, "The formation of the perithecium is initiated by the massing of the hyphae into a circular knot, within the center of which 'Woronin hyphae' differentiate. The ascogonia develop from the cells of the 'Woronin hyphae' by rounding out, partially separating from each other, and increasing in size. The ascogonia do not drop to the bottom of the perithecium in the older stages, but come to lie comparatively close to the bottom by an expansion of the perithecial wall toward the periphery of the stroma."

Fuisting (9: 305) found four stromatic types of *Hypoxylon* represented by *H. cohaerens*, *H. coccineum*, *H. rubiginosum*, and *H. udum*. In the first two the entostroma is well developed, forming an almost globose stroma. In *H. rubiginosum* the perithecia are seated in an entostroma, which is very thin, so that their bases almost touch the wood. *H. udum* first appears as a thin hyaline ectostroma on the surface of the wood, and without special differentiation is covered with a felt-like conidial growth, and after the development of the perithecia this ectostroma is seen as a firm black covering to the perithecia. There is practically no entostroma. The perithecia are seated directly in the wood. He says a striking similarity governs in the conidial formation in this genus.

Later (9: 307) he says one perithecial development serves for the family. In *H. cohaerens* the perithecial initial appears as a spherical ball, which is early differentiated into conceptacle and hymenial tissue, whose "Woronin hyphae" lie embedded at the base of the first formed knot, a thin thread-like, irregular weft, firmly coiled. Paraphyses form from all the inner wall layer accompanied by delicate paraphyses. The black tissue

over the stroma plays the rôle of a second covering to the perithecia. After a while the formerly spherical ball is changed by unequal growth into an upright, ellipsoid form, whose summit is perforated by converging tissue and becomes the ostiolum. He says the periphyses grow out from the basal cells resting on wall cells. Also the papilla grows up through the outer stroma.

The species of *Hypoxyton* studied by the writer can be placed in four distinct groups: (1st) Species with the mature stroma of woody texture, with red to purple ectostroma and dark-colored entostroma, and umbilicate ostiola—*H. Howeianum*, *H. coccineum*, *H. fuscum*, and *H. rubiginosum*. (2d) Species with carbonaceous stroma and an annular depression around the ostiolar papilla—*H. Malleolus*, *H. marginatum*, *H. annulatum*, *H. effusum*, *H. Michelianum*, *H. serpens*, and *H. illitum*. (3d) Species with very little to no entostroma and perithecia sunken in the substratum—*H. confluens*, *H. semiimmersum*, *H. udum*, *H. gregale*, and *H. Morsei*. (4th) Species with constantly effused, carbonaceous stroma (most of these are now in the genus *Nummularia*)—*N. Bulliardi*, *N. clypeus*, *N. punctulata*, *N. atropunctatum*, and *N. discreta*.

1. Stroma Woody, with Red to Purple Ectostroma and Dark-colored Entostroma, and Umbilicate Ostiola

HYPOXYTON HOWEIANUM Peck

The stroma is always globose to hemispherical and symmetrical, except when compressed by adjacent ones, and is never effused or pulvinate. Most stromata are 3–12 mm. in diameter and 3–8 mm. thick.

The color of the ectostroma is bright brick-red, and in later stages is very similar to that of *H. coccineum* Bull. In very old specimens this darkens to almost black. The monostichous perithecia are borne in the periphery of the stroma. The ostiolar papillae do not project out beyond the ectostroma, but in developing raise the ectostroma slightly over each perithecium. The opening is umbilicate. None of the body of the perithecium is erumpent through the outer stromal layer. The asci are about 80–100 μ in length, the spore part being from 50–60 μ long. The ascospores are from $3-3\frac{1}{2} \times 6-9 \mu$.

This species is most common on species of *Quercus*, particularly *Q. alba*, *Q. stellata*, and *Q. montana*, although it has been found on many other hosts.

Shear (27: 84) says *H. Howeianum* Peck is equal to *H. coccineum* Bull. The writer has examined Peck's type of *H. Howeianum*, and finds the asci are 80–100 μ in length, and the spores are $3-3\frac{1}{2} \times 6-9 \mu$. This specimen is on *Pyrus Malus*. *H. coccineum* has asci 120–150 μ long and spores $12-14 \times 5-7 \mu$. This is true in Exsicc. Moug. et Nestl., Stirp. Vog.-Rhen. no. 273, which is cited by Nitschke (19: 29) and also by Fries (7: 332). This is on *Fagus*. In the United States *H. coccineum* occurs on *Fagus* and the writer has never found it on another host. *H. Howeianum* occurs on several hosts, and apparently has not been found on *Fagus*. Shear further says *Sphaeria enteromela* Schw., in Michener's herbarium, is a form of *H. coccineum*, and that the specimen consists of two pieces, one on *Fagus* and one on *Castanea*. The specimen on *Fagus* is immature, but the one on *Castanea* contains spores of typical *H. coccineum*, which according to him are $10 \times 3 \mu$. The confusion here is due to the two species having been mixed in this packet, and the one on *Castanea* is *H. Howeianum*, and the one on *Fagus* is probably *H. coccineum*. The writer has seen many specimens of *H. Howeianum* on oak in various herbaria, all of which were labelled *H. coccineum*. The two are apt to be confused in certain stages unless one examines the spores.

In February 1926, the writer inoculated twigs and wood of *Quercus alba* with ascospores, and left them outdoors all of the following spring and summer. The next fall stromata of various degrees of maturity were found in abundance. Also conidia were plentiful during rainy weather. Free-hand sections, as well as paraffin, were made from time to time and the development studied.

The ascospore germinates on the bark and the germ tube penetrates the periderm, ramifying between that tissue and the cortex. From this very fine hyphal threads penetrate the cortex and xylem, and their limits become circumscribed by a black line. Next, this plexus of hyphae within the bark swells enormously, rupturing that tissue. The cells in this layer by coalescing form

a definite stroma. At this period these cells are angular, pseudoparenchymatous, and are bright orange in color. This layer is homologous with the ectostroma of *Diatrype stigma* (Hoffm.) Fries as described by Wehmeyer (31: 593). This ectostroma forms the outer coat to the developing entostroma.

The entostroma begins as a delicate pseudoprosenchymatous tissue directly under the ectostroma. At this time it is composed of fine parallel hyphae, about $3-4\ \mu$ in diameter. They appear steel-gray in color. These hyphae form a palisade layer with the growing point just under the ectostroma. Even at this stage there is a sharp line dividing these tissues. As growth proceeds here the bark is further ruptured and the young stroma appears, about 1-2 mm. in diameter.

Just as soon as the bark is ruptured and the air is let in, conidiophores appear on the ectostroma. The conidia are minute, about $4-6\ \mu$ in diameter, varying from globose to oblong, and are hyaline. They are borne in clusters of one to several on ends of branches. The cluster, or single spore, is forced to occupy a lateral position by a branch arising directly under it and growing upward. This development is common to the other *Hypoxylon* species. The ability to produce these conidia seems to be retained by the ectostroma throughout its life period. Mature stromata will become covered with this gray conidial layer in warm rainy periods during the winter. Plate 36, fig. 7, shows the manner of conidiophore branching.

Perithecial initials arise in the upper part of the entostroma just under the ectostroma. They are seen at an early stage and are carried upward with the growing palisade layer. At first a hyphal knot is noticed in this position. This grows in a peripheral manner and all the cells which ultimately compose the perithecium come from this knot. When this becomes about $30\ \mu$ in diameter, coiled deeply staining hyphae of large diameter appear in the center. These are "Woronin hyphae," and have been seen in all *Hypoxylon* species examined. They become closely septate and the segments give rise to ascogenous hyphae, paraphyses, and periphyses.

The perithecial centrum as exhibited by *H. Howeianum* is typical for this genus. (PLATE 36, FIG. 2.) The asci are located

at the base and sides of the perithecium, oriented toward the ostiolum. The ascospores are light brown, and lie uniseriately in the ascus. The wall of the latter is thin, hyaline, and not thickened at the tip. The asci are cylindrical and long stalked. The ascogenous hyphae give rise to from 8-15 asci. (PLATE 36, FIG. 6.) All do not mature at the same time. The paraphyses are very delicate and branched and at an early stage completely fill the centrum. Delicate periphyses line the ostiolum.

The texture of the stroma is constant even with old age. It is never brittle-carbonaceous as in *H. marginatum* or *N. Clypeus*. When young it is fleshy and in age it becomes leathery to woody. Other constant characters are the dimensions of the ascospores and asci and the bright brick-red color of the ectostroma.

HYPOXYLON RUBIGINOSUM Fries

The stroma in this species seems to be the most variable of all the *Hypoxylon* species. It is entirely plastic under different environmental conditions and this has led to much confusion. Many species have been created on these environmental forms. The writer has found no host specialization.

In February 1926, the writer inoculated species of *Fraxinus*, *Salix*, *Acer*, *Quercus*, *Castanea*, and *Viburnum* with ascospores. The inoculations were made on thick bark, very thin bark, completely decomposed bark, and on decorticated wood. In this manner many variations of form and color were gotten. Photographs taken from the resulting stromata are shown on Plate 35, figs. 5, 8, 9. The first is the purple-red form which has been called *H. fuscopurpureum* (Schw.) Berk. The second represents what has been considered as typical *H. rubiginosum*, and the third is typical of what is called *H. perforatum* (Schw.) Sacc.

The stroma is pulvinate or effused, indefinite in extent. On decorticated wood it is continuous for several inches, and often perfectly smooth with only a slight raise over each perithecium. On thick bark it is pulvinate and often resembles *H. fuscum*. (PLATE 35, FIG. 2.) The irregular pulvinate form seen in fig. 9 is on thin, very rotten bark. The perithecia often stand almost fully exposed on the stroma. Sometimes they are aggregated

and often they are entirely separate. In old age the ectostroma flakes off, exposing from one half to two thirds of the perithecial walls.

The young stroma is fleshy-leathery, at maturity woody, and in very old specimens crumbling. It is never carbonaceous and so can be sectioned.

The color of the stroma when young is bright brick-red to purplish-red to shades of reddish-brown, and it is extremely variable in these colors. The writer has found the color to be entirely dependent on the moisture content. The brighter colors develop under moist conditions and the drab-brown colors under dry conditions. In old age the stroma becomes black.

The interior of the ectostroma is always colored, while the entostroma is always dark. The entostroma may be highly developed when in thick bark, or often there is very little entostroma and the perithecia are oriented under a very thin ectostromatic layer.

The asci are 70-80 μ long for the spore part and 65-80 μ for the stalk. The latter is very long and filiform. The ascospores are 4-6 \times 9-12 μ .

The conidial layer arises from the ectostroma as described for *H. Howeianum*. In color and dimensions of conidia no distinction was found between this species and many others. During rainy weather the conidia develop on old stromata as well as on young. This layer disappears in dry weather, leaving the ectostroma smooth.

In old stromata the ostiola are stuffed with a white mycelial growth. This is the so-called distinctive character of *H. perforatum* and supposedly separates that species from *H. rubiginosum*. The writer found this condition more frequently with pulvinate stromata, but also often in effused ones. Shear suggested to the writer that this growth is due to germinating ascospores, and this has been found to be so. Therefore, as measurements of asci and ascospores and stromal characters of *H. perforatum* agree entirely with those of *H. rubiginosum*, the two must be identical.

The most distinctive characters of this species are the color and irregular growth of the stroma. It is more apt to be confused

with the effused form of *H. multiforme* Fries. However, the perithecia are larger in the latter and the ostiolar necks are always papillate, whereas they are umbilicate in *H. rubiginosum*.

Hypoxylon fuscum Fries will not be described here because in development it closely approaches the other members of this series. It is distinct in that it occurs only on *Alnus*, *Corylus*, and *Betula*.

The members of this series studied here are *H. Howeianum*, *H. coccineum*, *H. fuscum*, and *H. rubiginosum*. They are alike in having an ectostroma which is some shade of red or purple, in the woody texture of the mature stroma, and in possessing umbilicate ostiolar necks—that is, the perithecial neck does not project out beyond the ectostroma. The first two species are fairly constant in their subglobose form, whether erumpent from bark or on decorticated wood. These two can be separated on ascospore characters. *H. fuscum* and *H. rubiginosum* assume a form determined by the substratum. The last two can be separated on the measurements of ascus and ascospore, and usually on color of ectostroma and on host. No distinctive conidial characters were found.

2. Stroma Black, Carbonaceous, Ostiola Annulate

HYPOXYLON ANNULATUM (Schw.) Mont.

The stroma in this species is hemispherical when growing from bark and indeterminately effused when on decorticated wood. Plate I, fig. 10, shows the pulvinate type, and on Plate IV, fig. 5, is a drawing showing a longitudinal section of such a stroma. The color of the young stroma is tobacco-brown, and at maturity it is black. The apices of the perithecia are flattened into a truncate disk with the papillate ostiolar necks in the center. The perithecia are large, nearly globose, and about 1 mm. in diameter. The asci are cylindrical, sp. p. 60–70 μ in length, and with a stalk 35–40 μ long. The ascospores are uniseriate, inequilaterally elliptical, 3–4 \times 7–9 μ , and dark brown at maturity.

After inoculation with ascospores tobacco-brown mycelium arises on decorticated wood, or when the inoculation is made on bark, between the bark and the cortex. This coalesces to

form an ectostroma. When on wood it is loose, subiculum-like, and has the appearance of a similar structure in *Rosellinia aquila* (Fries) De-Not. When under the bark it swells and breaks the latter, becoming erumpent by the developing palisade layer of entostroma under it. The perithecia arise in the periphery of the entostroma.

The conidial layer arises from the ectostroma as a thick, brown subiculum. The conidiophores are much branched, giving rise to spores as described for the other species of *Hypoxylon*. The only distinctive character here is the thick, subiculum-like growth, and the brown color. The spores are similar to other species of *Hypoxylon*.

The texture of the mature stroma is very hard and carbonaceous. It is impossible to section this species.

H. annulatum occurs on members of the white oak group. The writer has found it only on *Q. alba*, *Q. stellata*, and *Q. montana*.

The point of special interest with this species is the development of the annulate depression around the perithecial necks. The drawing on Plate IV, fig. 5, shows what occurs. The developing perithecia in this *Hypoxylon* group grow through the ectostroma to the extent of the ring. The top of the perithecium breaks through and the margin of the ectostroma produces the circular depression.

HYPOXYLON MARGINATUM (Schw.) Berk.

The stroma at maturity is black, semipulvinate to hemispherical, very variable in form, 1-4 cm. in diameter and 2-10 μ thick. It is never flat and effused. The surface is slightly roughened by the annular depressions. The asci are cylindrical, with sp. p. 65-75 μ and stalk 40-50 μ . The ascospores are uniseriate, slightly inequilaterally elliptical, 3-4 \times 7-9 μ , and at maturity are opaque.

The young stroma is olivaceous-green inside and darker on the outside with a greenish tint. The conidial layer is also of that shade. This species never forms a thick subiculum as in *H. annulatum*. In young stages the stromata are nearly globose, with an even surface, showing no evidence of perithecia, the latter breaking through the ectostroma late in the development.

The entostroma is always well developed. From inoculations on decorticated wood no flat effused forms were gotten from *H. marginatum*, but *H. annulatum* did produce an effused form.

The conidia are produced as in other species of *Hypoxylon*, and are about $4 \times 3 \mu$ in diameter and hyaline to greenish-hyaline.

This species occurs on a variety of hosts. The writer has found it on *Quercus velutina*, *Q. nigra*, *Q. borealis*, var. *maxima*, *Acer rubrum*, and *Betula nigra*.

Shear (27: 84) says *H. annulatum* is equal to an effused form of *H. marginatum*. After studying these closely in the field the writer has found no intergrading forms, and the differences in color of young stromata, presence of a subiculum in the former and not in the latter, differences in hosts, and constant differences of development, are certainly sufficient to maintain them as distinct species.

HYPOXYLON EFFUSUM Nits.

The stroma is indefinitely effused, convex, black at maturity, and dotted by the exposed annular disks as in the two previously described species. In old stromata the ectostroma wears off, leaving the perithecia exposed. The condition varies then from a thin, widely effused one, which resembles a smooth form of *Nummularia Bulliardii* Tul., to one of simple perithecia in old specimens, such as are seen in forms of *Rosellinia*. The asci are cylindrical, attenuated into a stalk. The spore part is $50-60 \mu$ long and the stalk is $30-40 \mu$. The ascospores are uniseriate, $5-8 \times 3-3\frac{1}{2} \mu$, and at maturity are pale brown.

This species occurs in the tropics and in the Southern States.

The *H. effusum* studied here is the same as Saccardo understands it in *Myc. Venet. 1470*, and not the same as the Ellis specimen on *Ulmus*, N.A.F. 2114. The latter is a form of *H. serpens* Fries.

The constant characters here are the small spores, the very flat, effused stroma, developing under the bark in large sheets as in *N. Bulliardii*, and the lack of entostromatic development as found in *H. annulatum* and *H. marginatum*.

Hypoxylon polyspermum Mont. has been made a synonym of

H. effusum by Theissen (28). He separates *H. annulatum*, *H. marginatum*, and *H. effusum* in that paper on spore and perithecial measurements. The fact that all of them show the annular depression around the ostiolar papillum and have spores very close in measurements has led to much confusion.

H. Michelianum Ges. & De-Not. and *H. malleolus* Berk. & Rav. are black and have this ostiolar circular depression. The former is irregularly pulvinate and the latter is constantly globose to subglobose. They occur in the Southern States and in Porto Rico.

H. serpens Fries and *H. illitum* (Schw.) Sacc. have a carbonaceous ectostroma and sometimes an annular depression is visible around the ostiolar papilla. These two species are transitions between this series and the next.

3. No Entostroma, Perithecia Sunken in the Substratum, Ostiola Papillate

HYPOXYLON MORSEI Berk. & Curt.

In this species the stroma is 3-5 mm. in diameter, flattened above, partially erumpent, and is composed of from 5-10 perithecia. The latter are large, about 1 mm. in diameter, globose, and flattened on top. The asci are cylindrical, 120-140 sp. p., and the stalk is 40-60 μ long. The ascospores are uniseriate, elliptical, with rounded to acute ends, and measure 17-22 \times 8-10 μ . A mature stroma is shown on Plate I, fig. 6.

There is a thin ectostroma covering the perithecia and there is practically no entostroma. The bases of the perithecia are sunken in the wood.

This species occurs on *Corylus* and *Salix*.

HYPOXYLON GREGALE (Schw.) Berk.

The mature stroma is black, semiimmersed in the bark, slightly erumpent, hardly as much so as in *H. Morsei*, and is 2-3 mm. in diameter. The surface is smooth except for the papillate erumpent ostiolar necks. The perithecia are flask-shaped, $\frac{1}{2}$ mm. in diameter. The asci are cylindrical, 75-80 μ long for the spore part and 20 μ for the stalk. The spores are

uniseriate, elliptical, $7-9 \times 12-14 \mu$, and at maturity are opaque.

This species lies near *H. Morsei*, in that the perithecia are seated directly in the wood, and so there is practically no entostroma. In both the stromata are flat, but very definite in outline.

HYPOXYLON UDUM (Fries) Nits.

The stroma is flat, orbicular, 4-5 mm. in diameter or less, and about 1 mm. thick. When young the ectostroma is light clay colored, varying to brown at maturity and almost black on old stromata. The young stromata are soft and fleshy and mature ones are membranaceous to woody. They are easily sectioned. The asci are $140-160 \mu$ long for the spore part and $25-35 \mu$ for the stalk. The ascospores are $22-28 \times 10-12 \mu$.

The conidia are hyaline, oblong to globose, and $4-6 \times 4 \mu$. The general characters of the conidial layer are similar to those found in other *Hypoxylon* species.

HYPOXYLON SEMIIMMERSUM Nits.

The young stroma is very similar to that of the above species. The ectostroma is first seen as a light gray, very thin layer. The perithecia arise under this in the woody tissue. The mature stroma is $4-5 \times 2-3$ mm., and is flat with only the ostiolar papillae projecting, or individual perithecia are visible. Often the perithecia are serially arranged in the medullary crevices and are connected only by a very thin ectostroma. There is no entostroma. The asci are $80-90 \mu$ long for the spore part, and $60-70 \mu$ for the stalk. The ascospores are $17-19 \times 6-8 \mu$, and elliptical with rounded ends.

The conidiophores form a light gray layer over the ectostroma. The conidia are hyaline and $5-8 \times 3-5 \mu$.

This form occurs at Ithaca on decorticated wood, and has been found only on *Quercus*. Rehm determined this as *H. udum* Fries, but the spores are too small for that species. In spore dimensions it is intermediate between *H. udum* and *H. serpens*.

HYPOXYLON CONFLUENS (Fries)

In this species the perithecia are also seated directly in the wood, but instead of forming sharply delimited stromata, they

are practically free (PLATE 35, FIG. 7). Each perithecium is covered with an ectostroma, as in the genus *Rosellinia*. The stroma consists of from 5–10 perithecia united by their bases.

This series comprises most of the forms placed in the subgenus *Endoxylon* Nits. The constant characters are the small, flat, membranaceous stromata, the partially sunken perithecia with practically no entostroma, and the papillate perithecial necks. The last character separates these species from the effused ones in the first series, and the membranaceous texture of the stroma from effused species in the second group. The differences in ascospore dimensions are sufficient to separate the species.

NUMMULARIA DISCRETA (Schw.) Tul.

It is impossible to place this species in any one of the four series considered here. However, it will be discussed at this point because it appears to be intermediate between the third and fourth series, but it also has affinities for the genus *Anthostoma*.

The stromata are concave, sunken below the bark, definite in outline, and 3–5 μ in diameter. The perithecia are sunken in the stroma, and reach the surface by long ostiolar necks as in the genus *Valsa*. The asci are cylindrical, short-stalked, 160–200 \times 12–15 μ . The spores are globose, black at maturity, 12–14 μ in diameter, and uniseriate in the ascus.

A light-colored ectostroma composed of angular pseudo-parenchymatous cells develops between the bark and cortex. Under this a valsooid entostroma arises. This is composed of wood mixed with hyphae, and is limited by a black line. It is not a stroma in the sense of most species of *Hypoxylon*. Initial coils in this entostroma produce globose perithecia that grow outward into long necks. The latter penetrate through the ectostroma (PLATE 36, FIGS. 3, 4). Before this development is completed the ectostromatic cells swell and rupture the bark. Just as soon as the bark is broken, so air can get in, the upper surface of the ectostroma becomes covered with a hyphomycetous conidial growth. The conidia are continuous, hyaline, and are borne in the same manner as in the genus *Hypoxylon*.

Tulasne (30: Tab. 5, figs. 2 and 14) pictures the conidia in this species and in *N. Bulliardii* Tul. as arising under a definite

stromatic layer, and this illustration has been the basis for separating the genus *Nummularia* from *Hypoxylon* since his publication. As described above, the writer has found that the conidia arise on the ectostroma in the same manner as in the genus *Hypoxylon*. Cooper (4) in a letter to the writer says, "Conidia never appeared, however, except where cracks or perforations in the bark permitted the free access of air. I am quite certain that conidia were not formed before the free access of air under the blisters. At no time did I find conidia under a stromal layer."

This species with its long perithecial necks and valsoid stroma furnishes a transition towards the genus *Anthostoma*. It is quite different from other members of Tulasne's genus *Nummularia*, and also from any *Hypoxylon* species. The writer thinks it is best to leave it in the *Hypoxylon* group, rather than place it in *Anthostoma*, because there is more ectostromatic development here than in the latter genus.

4. Stroma Constantly Effused, Thin, Ostiola Papillate

NUMMULARIA CLYPEUS (Schw.) Cooke

The stroma is black, effused for several inches to several feet, erumpent from below the bark, convex, and resembles *N. Bulliardi*. The perithecia are globose to flattened where crowded, with short ostiolar necks which penetrate the ectostroma and are papillate on the surface. The asci are for the spore part 120–140 μ in length, and 20–30 μ for the stalk. The black ascospores are uniseriate, fusoid-elliptical, $9-12 \times 18-22 \mu$. The form and measurements of the ascospores as well as the thickness of the stroma will serve to distinguish this species from *N. Bulliardi*.

As in *Nummularia* and *Hypoxylon* species of this type the ectostroma spreads under the bark by coalescing and growing laterally for several inches to several feet. The perithecia are usually fully developed before the bark ruptures. When this breaks off it carries with it the part of the ectostroma which is mixed with bark cells and leaves a hard black crust. Conidia develop from any exposed stromatic surface during rainy weather. When the conidial layer disappears there is left a remnant

around the margin. This is also characteristic of *Hypoxylon* species.

HYPOXYLON ATROPUNCTATUM (Schw.) Cooke

This fungus has been placed in *Nummularia*, as well as in *Diatrype*. In development it certainly belongs along with *N. Bulliardi*.

The stroma is white, punctate with black ostiolar papillae, and widely effused. The perithecia are globose to flask-shaped, 200–300 μ in diameter. The asci are 150–160 \times 12–14 μ , with very short stalks. The ascospores are uniseriate, 25–30 \times 11–14 μ , at maturity black, and are elliptical with pointed ends. The paraphyses are filiform.

This species is very common on oaks in the Southern States.

The ascospore sends a germ tube into the bark which ramifies and develops a wide mycelial plexus, which coalescing with other infections produces a layer several feet in length. A black circumscribing line delimits each stroma (PLATE 39, FIGS. 1, 2, 3).

When sufficient ectostroma is formed between the bark and cortex it swells and bursts the bark in longitudinal cracks. As soon as the air enters, conidiophores arise from the upper surface of the exposed ectostroma. The bark now falls off in large strips, exposing the gray conidial layer. The conidiophores produced in cracks of the bark are very long and branched and produce masses of globose conidia about 5–6 μ in diameter. This species is remarkable in that the pulverulent conidial layer is found all during the summer and does not disappear in dry weather as is the case with other species of *Hypoxylon* (PLATE 38, FIGS. 1, 2).

The entostroma is very thin, and the perithecia are almost in contact with the wood. The upper surface is covered with the white ectostroma. This layer is very hard and carbonaceous (PLATE 35, FIG. 4, and PLATE 38, FIG. 4).

In very old stromata the white layer on top peels off entirely or in patches, leaving a black entostroma exposed. Then this species is confused with *H. stigmatum* Cooke and is probably identical with it.

NUMMULARIA PUNCTULATA (Berk. & Rav.) Sacc.

The stroma here is widely effused as in the preceding one, developing under the bark, and at maturity throwing it off in wide sheets. Most of the ectostroma peels off at maturity, leaving the surface smooth and shining as if glazed. The perithecia are globose to flask-shaped. Very few of them produce asci. The latter are small, cylindrical, and the spore part is $45-55\ \mu$ and the stalk is $30-40\ \mu$. The ascospores are light brown, uniseriate, elliptical, $3-4 \times 7-9\ \mu$. The peculiarly constant character in this species is the fact that the ostiolar necks rarely grow entirely through the ectostroma. They resemble needle pricks in a smooth surface.

The conidia develop on any exposed stromata during rainy weather. The spores are hyaline and $3-3\frac{1}{2} \times 6-8\ \mu$.

The writer placed pieces of this species in a moist chamber and after several weeks the surface of the stroma was covered with papillae just as in other species of *Nummularia*. When sectioned this material revealed all the perithecia filled with asci. From this it would seem that the perithecial necks failing to come through is correlated with a lack of ascus development.

Nummularia tinctor (Berk.) Ellis & Ev., *N. hypophloea* (Berk. & Rav.) Cooke, and *N. microplaca* (Berk. & Curt.) Cooke were also studied in the field and in the laboratory, and as they develop in the same manner as the ones described above they will not be discussed further.

As the writer has stated previously, the one difference between the genus *Nummularia* and *Hypoxylon* according to Tulasne is the substromal conidial layer in the former and not in the latter. Now that the writer has shown that the conidial layer arises in the same manner in both genera, it is only logical to place the species that were taken out of *Hypoxylon* and placed in *Nummularia* back in *Hypoxylon*. To maintain the genus *Nummularia* there should be at least one difference which is constant for the majority of species in the two groups. The writer knows of no such difference. The majority of forms now included in *Hypoxylon* are effused as often as they are pulvinate. The globose or hemispherical forms are exceptional.

The members of this series are characterized by being con-

stantly flat and effused, with very little entostromatic development, but the perithecia do not rest directly in the wood. In texture the stroma is always carbonaceous, and so it is impossible to section. The ostiolar necks are papillate in all the species studied except *N. discreta* and *N. punctulata*. The writer considers the former a transition form to *Anthostoma*, and so not a good member of this group. *N. punctulata* has papillate ostiolar necks when there is ascal development, and so should be included here.

Effused forms of *H. rubiginosum*, such as those which have been named *H. suborbiculare* Peck and *N. lateritia* Ellis, have the same type of development.

ROSELLINIA Ces. & De-Not.

In this genus the characters of the perithecial centrum are exactly the same as found in the Xylariaceae. It was placed in the Sphaeriaceae by Lindau (16: 394), because he thought the perithecia were free, that is, superficial and not stromatic.

ROSELLINIA AQUILA (Fries) De-Not.

Inoculations of wood of *Carpinus caroliniana* were made in Feb. 1926, and the development was studied. A definite ectostroma forms in the bark and ruptures it. This gives rise to a subiculum of brown hyphae which grows out through the ruptures and, after coalescing, forms a more or less indefinite mat on the outside of the bark. Conidia arise on this subiculum in the same manner as in the genus *Hypoxylon* (PLATE 37, FIGS. 1, 2, 3, 4). Next a well-developed entostroma, composed of elongate parallel hyphae, forms under the ectostroma. In its periphery one or more perithecial initials develop. The growing perithecium pushes up the ectostroma, the subiculum disappears, and the mature perithecium is tightly fitted within an outer ectostromatic layer (PLATE 36, FIG. 8). Ellis (6: 163) says there is an outer, rather thick but brittle carbonaceous wall, and an inner coriaceous one. The perithecial neck grows through the ectostroma as in *Hypoxylon*.

The conidiophores are irregularly branched. Apical conidia are cut off, then the hypha elongates from under the conidium

in a vertical direction and produces another conidium, and so on (FIG. 4). The conidiophores and conidia are greenish-brown in color, oblong, and variable in size, $2-3 \times 5-8 \mu$.

Rosellinia subiculata (Schw.) Sacc. develops in exactly the same manner as *R. aquila*. PLATE 37, FIG. 5, shows a mature perithecium oriented under an ectostroma. The subiculum has disappeared. In this species there is no well-developed entostroma.

The perithecia of *Rosellinia Clavariae* (Tul.) Wint. (PLATE 37, FIG. 6) differ from those of most other *Rosellinia* species in that there is no entostroma and the ectostroma at maturity forms a tight coat on the outside of the perithecial wall. This condition is fully equal to an illustration of *Sordaria* sp. by Gwynne-Vaughan (11: 138, fig. 100).

Forms now placed in the genus *Rosellinia* have the same type of development as those in the genus *Hypoxylon*. Also they are definitely connected with the genus *Hypoxylon* by such transition forms as *H. confluens* and *H. annulatum*. However, as long as the majority of *Rosellinia* species have single perithecia in the stroma and the majority of *Hypoxylon* species have many, it is desirable to separate these two groups; that is, to continue them as separate genera, but they should certainly be in the same family.

USTULINA Tul.

This genus was founded by Tulasne (30: 23) on *Hypoxylon ustulatum* Fries and was segregated on account of its fleshy conidial layer.

A longitudinal section through a young stroma of this species is shown in PLATE 36, FIG. 5. The conidial layer forms on the outside of the ectostroma (FIG. 5b). At this stage young perithecial initials appear (FIG. 5c). After further growth the perithecia come to occupy most of the stroma, the conidial layer disappears, and the ectostroma remains as a black, carbonaceous layer over the perithecia. The perithecial centrum characters are similar to what is seen in *Hypoxylon*.

The development in this genus is exactly the same as in *Hypoxylon*. The fleshy texture of the young stroma is not limited to *Ustulina*, as all *Hypoxylon* species are fleshy when

young. The gray color of the immature stroma is not a character of generic importance, as *Hypoxylon* species in this stage vary from white to shades of red, purple, and so on. If the color, or the form of the stroma, is sufficient to maintain the genus *Ustulina*, then the present genus *Hypoxylon* could with equal propriety be broken up into as many genera as there are now species. Therefore, it is suggested that members of this genus be placed back in *Hypoxylon*.

DALDINIA De-Not.

Forms of *D. concentrica* (Bolt.) Ces. & De-Not., *D. Eschscholzii* (Ehr.) Rehm, *D. vernicosa* (Schw.) Ces. & De-Not., and *Hypoxylon placentiiforme* Berk. & Curt. have been studied.

A grayish-brown ectostroma becomes erumpent through crevices in the bark, or when on decorticated wood this stromal growth occurs irregularly effused on the surface. Under the ectostroma a dark-colored entostroma soon develops, pushing the former upward. Sections of young stromata 1 to 2 mm. thick show a peripheral layer of perithecial initials oriented just under the light-colored ectostroma. At this stage the condition is identical with that found in such *Hypoxylon* species as *H. coccineum* and *H. Howeianum*. There is no indication of concentric zones under the perithecial layer. By studying a series of forms, beginning with one with one perithecial layer and ending with one with many concentric zones (PLATE 36, FIG. 1), the writer found that the first series of initials disintegrates and meristomatic hyphae from below grow upward and around these coils and produce another series of initials. This action continues until from six to forty such zones are formed. Finally, when the last initials develop into perithecia the zonation ceases. The concentric zones then in *Daldinia* are apparently formed from perithecia which are arrested in their development and disintegrate.

All of the *Daldinia* species mentioned above have certain characters in common besides the concentric zonation. The conidial layer is a light grayish-brown in all four species. The conidia are hyaline, with a slightly greenish tint, and are 6-8 \times 4-5 μ , and are borne on sympodially branched conidiophores.

The color of the mature ectostroma, after the conidial layer disappears, is a dark purple. The perithecial necks do not penetrate through the ectostroma, so the ostiola are umbilicate. The ascus and ascospore measurements are very close together in the four species. The differences are found in the forms of the stromata. *D. concentrica* is usually sessile and centrally attached, varying to forms that are plainly stipitate. *D. vernicosa* is laterally compressed, plainly stipitate, and tends to become hollow inside, due to gelatinization of parts of the ectostroma. *D. Eschscholzii* is similar to *D. concentrica* in all points except size. It is usually much larger than the latter and tends to spread out at the base. *H. placentifforme* (this is a true *Daldinia*) develops an irregular flat stroma with forms running into *D. Eschscholzii*.

The development in the above species in all fundamental characters is sufficiently similar to that in *Hypoxylon* to indicate a very close relationship, but the concentric zonation is so striking that it would appear best to continue the genus *Daldinia*.

ANTHOSTOMA Nits.

This genus is placed in the Valsaceae by Lindau (16: 455). He separates it from *Valsa* on spore characters. In *Anthostoma* the spores are brown and not allantoid. The stromatic characters are the same in the two genera.

Nitschke (19: 110) separated the genus into two subgenera, Euanthostoma and Lopadostoma. In the first he places species which are effused and usually inhabit decorticated wood, and in the second subgenus he places clustered forms.

Wehmeyer (31: 638) emends the genus *Anthostoma* and places it in von Höhnelt's family Allantosphaeriaceae. He says the perithecia are separately erumpent (Euanthostoma), or clustered and collectively erumpent (Lopadostoma). The ostiolar necks are irregularly sulcate or merely punctate. The spores are brown, allantoid to cylindrical or usually inequilaterally elliptical and one-celled.

In *Anthostoma gastrinum* (Fries) Sacc. the writer finds the perithecia are single or in valsoid groups in long lines in cracks in the bark (PLATE 38, FIG. 9). The asci line the base and sides

of the perithecium. They are cylindrical, stalked, with uniseriate, dark brown ascospores. The paraphyses are thread-like and similar to those in *Hypoxylon*. Periphyses line the ostium.

Anthostoma grandineum (Berk. & Rav.) Sacc. occurs on oak bark (PLATE 38, FIG. 6). The perithecia are in a definite stroma and the development is similar to that of *Hypoxylon*. This species differs from most *Hypoxylon* species only in its microscopic proportions. It should be in the genus *Hypoxylon*.

Anthostomella minor (Ellis & Ev.) (PLATE 38, FIG. 8) exhibits a so-called clypeus, which in this case is due to a combination of ectostroma between the outer cells of the host and a blackening of these cells. There is no definite stromal plate surrounding the perithecial necks. Both ectostroma and entostroma are poorly developed as in the members of the genus *Anthostoma*. The perithecial centrum characters are similar to *Anthostoma* and *Hypoxylon*. The only difference between members of this genus and those of *Anthostoma* is a tendency for the perithecia to be isolated in the former and aggregated in the latter. The writer thinks this tendency is not sufficiently striking to maintain them as separate genera, and suggests that the species now in *Anthostomella* be placed in *Anthostoma*.

The writer also thinks the genus *Anthostoma* should be placed in the Xylariaceae. The perithecial centrum characters are exactly the same as members of the genera *Hypoxylon*, *Xylaria*, etc. The difference is entirely a difference in the amount of stroma present. Here the ectostroma is hardly sufficient to rupture the bark, and this is accomplished by the upward growing perithecial necks. The entostroma is also poorly developed, being valsoid in that it is mixed with wood. Members of this genus closely approach such *Hypoxylon* species as *H. udum*, *H. semimmersum*, and *N. discreta*. In all of these the perithecia are seated directly in the wood, with only a thin ectostroma uniting them.

Petrak (23: 253) says *Anthostoma* stands in no close relationship with genuine *Valsa* species, and that the centrum cannot be distinguished from that of *Rosellinia* nor *Hypoxylon*. Further, he says that *Rosellinia*, *Creosphaeria*, *Leptomassaria*, *Antho-*

stomella and *Anthostoma* stand in a genetical series with the Xylariaceae and truly form a sharply characterized group through the form of the centrum and spores. Also he says there is no sharp distinction between *Anthostoma* and *Anthostomella*.

The species of *Anthostoma* represent the most primitive forms in point of stroma in the Xylariaceae, and probably are transition forms between this family and the Allantosphaeriaceae.

Discussion

These developmental studies show most strikingly that the members of the dark-spored series have many characters in common. In spite of this, many of these genera have been placed in widely separated families on stromal characters alone by such investigators as Nitschke (19), Cooke (3), Lindau (16), and Ellis (6). Orton (21: 50) says: "The presence or absence of stroma has been long regarded as a basis for the delimitation of systematic groups of major rank, but it seems clear to me that with increasing knowledge this usage is quite indefensible since in many cases it separates what are obviously on phylogenetic grounds closely related species." Von Höhnelt (13, 14) uses many characters in the separation of major groups, and lays particular emphasis on those of the perithecial centrum. Further, von Höhnelt separates his families, Allantosphaeriaceae and Diaporthaceae, entirely on characters found in the perithecial centrum. The proof of the continuity of any group is whether the members have more characters in common with each other than with other forms, and the presence of numerous transitions which would tend to make it difficult to satisfactorily delimit genera.

In summarizing the characters common to this series they will be considered under: (1) The stroma, (2) development of the perithecium, (3) the perithecial centrum, and (4) the conidial fructification. The differences will also be discussed under these heads. They will be differences in the amount and form of stroma, in ascus and spore measurements, and in the relation of the stroma to the substratum.

1. **Stroma.**—The minimum stromatic development is found in the genus *Anthostoma*. The perithecia in this genus are never

encased in such a thick stromatic wall as most of the forms in *Rosellinia*, *Hypoxylon*, etc. If the stroma is to be considered as indicative of phylogenetic development in this series, then *Anthostoma* is the most primitive, followed by *Rosellinia*, with transitions through *Rosellinia aquila*, into *Hypoxylon confluens*, *H. annulatum*, *H. semiimmersum*, *H. udum*, and so to ones with much entostroma such as *H. Howeianum*. Then from other *Hypoxylon* species such as *H. leucocreas*, which is white inside but patellate, we can go by a perfect series of transitions into *Xylaria*. The transitions in this series are so complete that any genera erected on the amount or form of the stroma will be only approximate.

This condition has been recognized by many investigators. Theissen (29), in discussing the question of species grouping in, the Xylariaceae, shows the uncertainty of separation between *Xylaria* and *Hypoxylon*, and says the single separation character is the stalk formation, which in itself alone in other fungous groups is not sufficient for generic separations, e.g., Pezizales, and even with the Xylariaceae as in *Daldinia* (some are stalked and some are not). The proof for this is in the presence of transition forms, from the central attachment and pseudo-stipitate constriction of the lower side of the stroma up to the plain stalk formation in different species and even in the same species; as for example with *Xylaria obovata*, *X. anisopleura*, *X. allantoidea*, *X. apiculata* and others. The genus *Daldinia* is united with *Hypoxylon* through *H. Petersii*, *H. exurgens*, *H. placentiforme* and others. Even *H. coccineum* and *H. Howeianum*, which are considered typical of *Hypoxylon*, show a plain concentric zonation in thin sections.

2. **Development of the Perithecium.**—In all the forms studied here, that is, in *Rosellinia*, *Anthostomella*, *Anthostoma*, *Hypoxylon*, *Daldinia*, *Ustulina*, and *Nummularia*, the perithecia are initiated by a coiled hypha, which on further growth develops a definite wall and "Woronin hyphae" on the inside. Elements of this wall grow upward, producing the perithecial neck. Brown (1) observed this development in *Xylaria*, and Dawson (5) in *Poronia*. In most of the species the perithecia are globose to flattened when crowded with very short papillate necks. The exceptions

are to be found in *Nummularia discreta* and *Anthostoma* species which have elongate necks, and in *Camarops* species which have elongate, compressed perithecia.

3. **Perithecial Centrum.**—The inside of the perithecium at an early stage is filled with "Woronin hyphae" which come to lie on the inner face of the wall. Then from this wall layer there arise paraphyses and later asci. Also periphyses arise from cells lining the wall of the neck. There is no pseudoparenchyma inside of the wall. At maturity then the perithecial centrum exhibits asci and paraphyses lining the base and sides of the wall and periphyses in the ostiolum. The asci are cylindrical and thin walled. The ascospores vary from light brown to black and are uniseriate in the ascus. They have a hyaline depression in the exospore, through which the germ tube is extruded. The shape of the ascospores varies from fusoid to inequilaterally elliptical to globose.

4. **Conidial Fructification.**—The conidia in species studied here are borne on hyphomycetous conidiophores, developing sympodially, singly or in clusters. All conidia are unicellular and very small. The conidiophores arise on an ectostroma which develops before the perithecia. The differences in conidia are not marked. In *Rosellinia* they are a little larger and darker than in *Hypoxylon*. In the latter genus very few differences in conidial dimensions were found which would aid in species determination. However, there are differences in color of the conidial layer and underlying ectostroma in a few species. *Xylaria* according to Brown (1) and *Poronia* according to Seaver, Whetzel, and Westcott (26) have the same general type of conidial development as the forms studied by the writer.

The Question of Generic Separations

In the Xylariaceae according to Lindau (16: 480) the generic separations are based on the form and texture of the stroma in all cases except for *Nummularia*, which was supposed to have conidia arising under a stroma, and *Camarops* and *Xylobotryon*, which should have two-celled ascospores. The writer has shown that the conidia in *Nummularia* develop in the same manner as in *Hypoxylon*. *Camarops* has been shown to have one-celled

ascospores by Theissen (29) and to equal *Bolinia*. *Xylobotryon* was examined by the writer and it has two-celled ascospores which are biseriate in clavate asci, and so clearly does not belong in this series. Theissen (29) sees no genetical differences between *Hypoxylon* and *Ustulina*, and says in *Ustulina* the form of the conidial layer furnishes no basis for generic separation. Lindau (16: 481) separates these two genera as follows: "... young stroma from the beginning thick and fleshy, covered with a conidial layer, at maturity carbonaceous . . . *Ustulina*; stroma from the beginning woody or carbonaceous . . . *Hypoxylon*." Theissen says further that this principle cannot stand in the face of so many *Hypoxylon* species which in the young condition are fleshy. The writer has found the stroma in all species of *Hypoxylon* studied to be just as fleshy when young as that of *Ustulina*. So this genus should be merged with *Hypoxylon*. This leaves the separations of the remaining genera to be based on the characters of the stroma.

There are no conidial characters nor perithecial centrum characters which are common to groups of species. The differences in stromal development will represent only the most striking tendencies, and so these will not make distinct separations. The most obvious fact about all the forms in this series is the great variability of the stroma to the environment. When on bark many *Rosellinia* species are immersed, and when on hard decorticated wood they are superficial. Also one often finds two or three perithecia in the stroma. This is not done by individuals coalescing but by several perithecia developing in the single stroma as shown previously for *R. aquila*. All *Hypoxylon* species arise from under the bark when there is any; otherwise they are entirely superficial. Most of them are effused on decorticated wood, and pulvinate to hemispherical when erumpent from bark. *Hypoxylon rubiginosum* is probably the most common species. Its environmental forms have been made the basis for many species found over the world. The transitions between *Hypoxylon* and *Xylaria* are now placed in the genus *Penzigia*. That procedure causes much confusion, because these forms are not constant for any one type. *Xylaria anisopleura*, as seen by the writer, varies in any one collection from globose-

sessile to slightly stalked to forms 2 or 3 cm. high, which are plainly stalked. The much branched condition seen in *Thamnomycetes* is common only in a lesser degree in many *Xylaria* species. So, as there are no constant stromal characters to separate genera the separations will have to be based on the most striking developmental tendencies. The writer suggests the following limitations of genera.

Anthostoma will be limited to all forms which contain perithecia with very little stroma, single or aggregated, which are sunken in the substratum. This genus will also contain species formerly placed in *Anthostomella*.

Rosellinia will be limited to forms with single perithecia which are superficial. In the genus *Sordaria* are many forms which should properly belong here. Most of them show no deviation from the illustration of *Rosellinia Clavariae* (PLATE 37, FIG. 6). The thickness or thinness of the stromatic layer on the outside of the wall is certainly not sufficient reason to exclude forms that have the Xylariaceae type of perithecial centrum. Also in the genus *Melanospora* and *Neurospora*, now in the Hypocreales, there are forms that are undoubtedly more closely related to *Rosellinia* than to the other members of the families in which they stand at present. They should be merged with *Rosellinia*.

Daldinia will be limited to pulvinate to globose forms, which are dark inside, and in which the stroma is conspicuously zonate.

Hypoxylon will be limited to effused to globose forms, which are not stipitate and not conspicuously zonate. This genus will include forms now in *Nummularia* and *Ustulina*, as well as all of those in *Hypoxylon* as it is now conceived.

Xylaria will be limited to forms with a stalked, clavate to globose stroma, which is usually white inside.

The other genera of the Xylariaceae have sufficiently distinct characters of the stroma to be easily segregated.

The writer proposes the following emended diagnosis for the family Xylariaceae.

XYLARIACEAE *emend.*

Asci long cylindrical, stalks long and filiform, or short, and asci almost sessile. Asci lining the bases and sides of the peri-

thecia. Ascospores unicellular, light-brown to black, inequilaterally elliptical, to fusoid, to globose, uniseriate in the ascus. Paraphyses threadlike, branched, completely filling the perithecial cavity at an early period, and more or less gelatinizing at maturity.

Perithecia membranaceous, seated under a more or less well-developed ectostroma, with the bases in entostroma.

Conidiophores hyphomycetous, covering an exposed ectostroma, branched; conidia single or in clusters, minute, borne apically and becoming lateral by continued growth of the conidiophore.

KEY TO THE GENERA

- Perithecia single or aggregated.
 - Superficial. *Rosellinia*.
 - Sunken in the substratum. *Anthostoma*.
- Perithecia several to many in the stroma.
 - Stroma effused, pulvinate to globose and sessile.
 - Internal zonation prominent. *Daldinia*.
 - Not conspicuous.
 - Perithecia elongate and strongly compressed. *Camarops*.
 - Not elongate nor compressed. *Hypoxylon*.
 - Stroma stalked, branched or not.
 - Stroma not flattened above.
 - Sterile portion of stroma not formed of strands.
 - Stroma deeply indented at the apex, bearing the perithecia in the infolded upper portion. *Camillea*.
 - Stroma otherwise.
 - Stromata capitate, crowded. *Kretzschmaria*.
 - Stromata clavate to cylindrical branched. *Xylaria*.
 - Sterile portion of stroma formed of strands, fertile portion clavate. *Thamnomycetes*.
 - Stroma broadened at the apex to form a flat shield-like termination. *Poronia*.

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EXPLANATION OF PLATES

PLATE 35

- Fig. 1. *Hypoxylon Howeianum* Peck.
 Fig. 2. *Hypoxylon fuscum* Fries.
 Fig. 3. *Nummularia discreta* (Schw.) Tul.

- Fig. 4. *Hypoxylon atropunctatum* (Schw.) Cooke.
 Fig. 5. *Hypoxylon rubiginosum* Fries forma *fuscopurpureum*.
 Fig. 6. *Hypoxylon Morsei* Berk. & Curt.
 Fig. 7. *Hypoxylon confluens* (Fries).
 Fig. 8. *Hypoxylon rubiginosum* Fries.
 Fig. 9. *Hypoxylon rubiginosum* Fries forma *perforatum*.
 Fig. 10. *Hypoxylon annulatum* (Schw.) Mont.

PLATE 36

- Fig. 1. Longitudinal section through a mature stroma of *Daldinia concentrica* (Bolt.) Ces. & De-Not.
 Fig. 2. *Hypoxylon Howeianum* Peck. Longitudinal section showing tendency to concentric zonation.
 Fig. 3. *Nummularia discreta* (Schw.) Tul. Longitudinal section through an immature stroma showing an ectostromatic layer between the periderm and the wood. The perithecia are seated directly in the wood.
 Fig. 4. *Nummularia discreta* (Schw.) Tul. Section through a mature stroma after the periderm has been thrown off.
 Fig. 5. *Ustulina vulgaris* Tul. Longitudinal section through an immature stroma. *a*, conidial layer. *b*, ectostroma. *c*, periphery of entostroma in which perithecia are developing.
 Fig. 6. Ascogenous hypha of *Hypoxylon Howeianum* Peck.
 Fig. 7. Conidiophores of *Hypoxylon Howeianum* Peck, showing sympodial growth habit.
 Fig. 8. *Rosellinia aquila* (Fries) De-Not. Longitudinal section through a mature stroma. *a*, ectostroma. *b*, entostroma. *c*, perithecial wall.

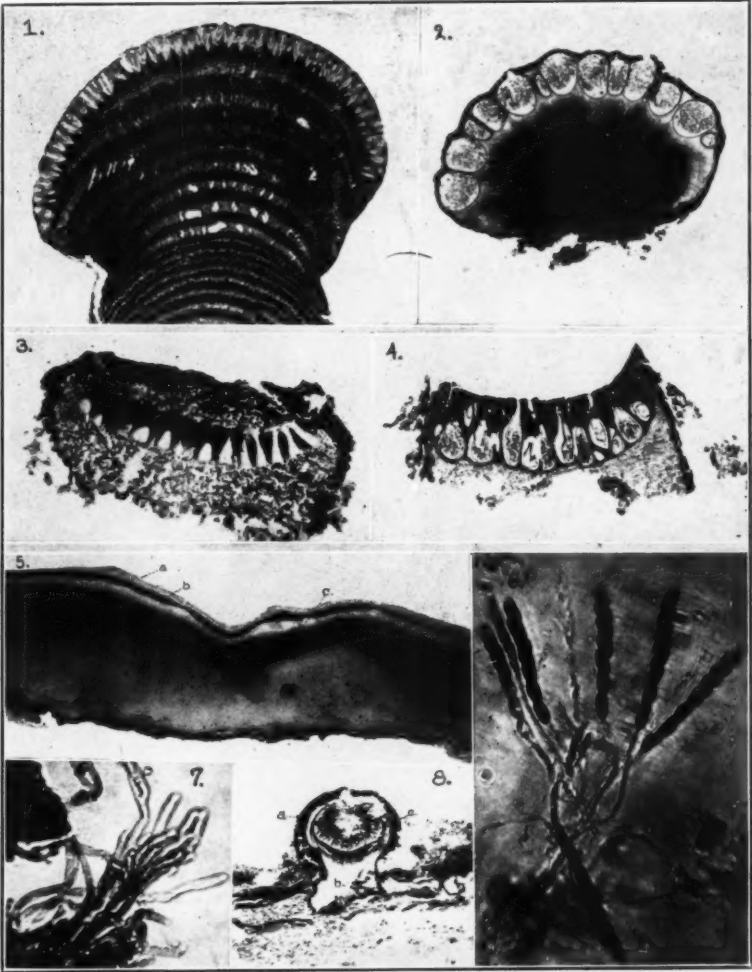
PLATE 37

Development in the genus *Rosellinia*.

- Fig. 1. *Rosellinia aquila* (Fries) De-Not. Longitudinal section through an immature stroma showing conidial layer rising from an ectostroma, and a well developed entostroma with perithecial initials in the periphery.
 Fig. 2. Longitudinal section showing further development of the above.
 Fig. 3. Longitudinal section through a mature perithecium. *a*, ectostroma. *b*, perithecial wall. *c*, conidial layer beginning to disappear. *d*, entostroma.
 Fig. 4. Drawing of conidiophores and conidia of *Rosellinia aquila*.
 Fig. 5. Longitudinal section of mature stroma of *Rosellinia subiculata* (Schw.) Sacc. The perithecium is seen to have developed under a very definite ectostroma with very little entostroma.
 Fig. 6. Longitudinal section through a stroma of *Rosellinia Clavariae* (Tul.) Wint. This mature perithecium is covered with large cells, some of which give rise to spines. This is the remnant of the ectostroma.

PLATE 38

- Fig. 1. *Hypoxylon atropunctatum* (Schw.) Cooke., showing ectostroma, covered with conidiophores, developed under the ruptured bark.
 Fig. 2. Conidiophores and conidia of the above.
 Fig. 3. *Hypoxylon annulatum* (Schw.) Mont. Conidiophores and conidia.

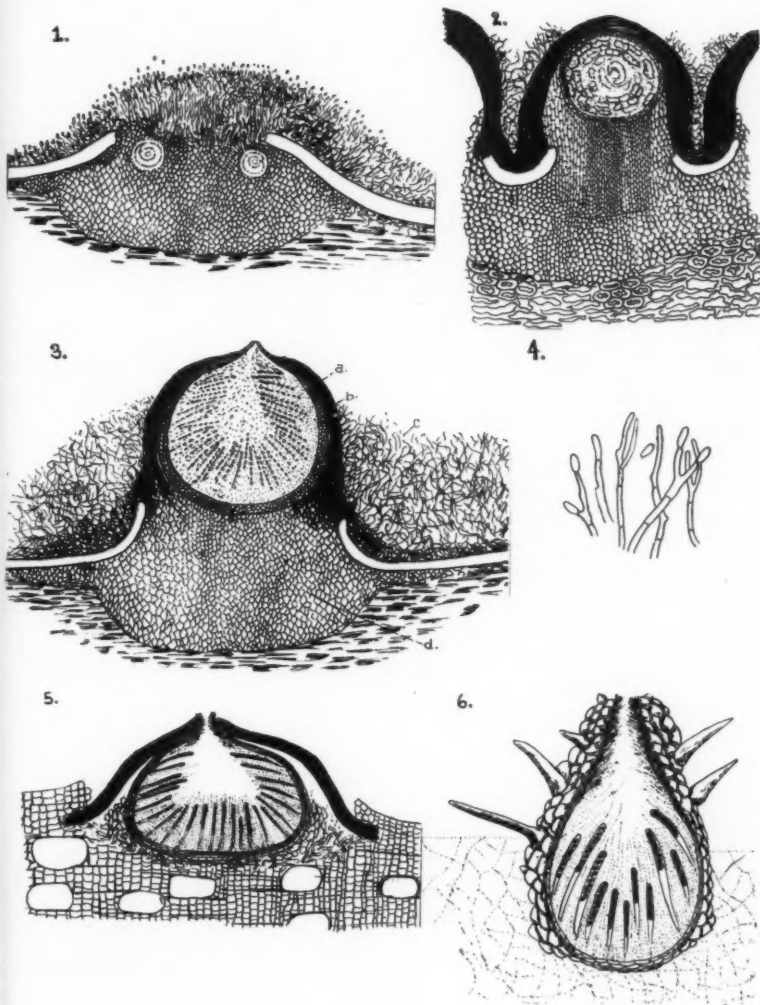


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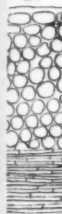
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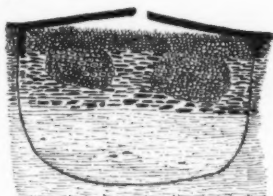
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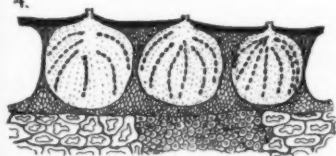
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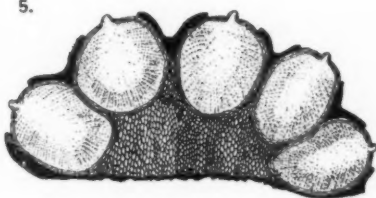
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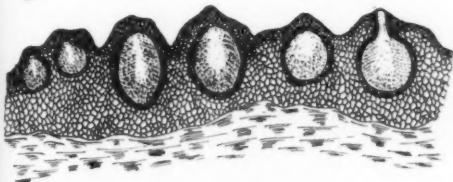
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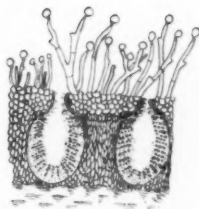
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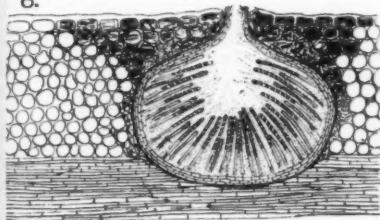
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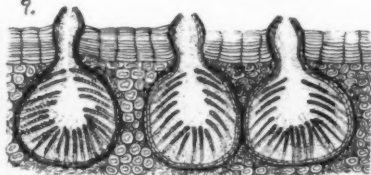
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XYLARIACEAE



Fig. 4. *Hypoxyton atropunctatum* (Schw.) Cooke. Section through a stroma showing habit of perithecia.

Fig. 5. *Hypoxyton annulatum* (Schw.) Mont., showing the cause of the annulate depression around the ostiolar neck.

Fig. 6. *Anthostoma grandinea* (Berk. & Rav.) Sacc. Longitudinal section through a mature stroma.

Fig. 7. *Nummularia punctulata* (Berk. & Rav.) Sacc. Longitudinal section showing conidiophores growing on mature stroma.

Fig. 8. *Anthostomella minor* Ellis & Ev. Longitudinal section showing the blackening around the ostiolar necks, the so-called clypeus.

Fig. 9. *Anthostoma gastrinum* (Fries) Sacc. Longitudinal section through several perithecia showing habit.

SOME OBSERVATIONS ON THE GERMINATION OF THE SPORES OF SOME SPECIES OF MYCETOZOA

W. R. IVIMEY COOK AND MISS E. M. HOLT

This work was commenced in order to investigate the germination of the spores of some species of Mycetozoa under artificial conditions. It had been generally found that germination is very variable, and that no certainty could be attached to the possibility of obtaining swarm spores when they are required for class work.

The statements found in Lister (5) and elsewhere, that the spores of various species germinate readily, could not be confirmed, and it was felt that certain physiological conditions must be necessary in order to achieve the results published.

During the autumn of 1927 sporangia of several species of Mycetozoa were collected in quantity from varying localities, and some preliminary experiments were carried out to test the time which must be allowed for germination to take place. It was at once obvious that this time factor differed very considerably in the species under observation. In *Reticularia Lycoperdon* germination occurred in about an hour, while in some species of the genus *Trichia* no germination was obtained in much under a week. Most species produce their sporangia in the winter when the temperature is low, on the other hand *Lycogola epidendrum* is found in a fruiting condition more or less commonly throughout the year. Experiments were therefore tried to determine what effect an alteration in the temperature, at which the germination was conducted had upon the number of swarm spores produced and the rapidity with which they appeared. The effect of light and darkness was also tested.

Some importance was also attached to the locality from which the material was collected; it was felt probable that some difference might be expected in the rate of germination in samples collected from different parts of the country. The number of varieties examined was to a large extent regulated by the quantity

of available material. In order to complete one series of experiments a very considerable number of sporangia was needed; it was therefore not possible to carry out experiments except upon those which could be collected in quantity. Five species were selected, and in four of these two separate series of germinations were used with material from different localities.

METHODS

The solutions in which germination was tried were selected from the results of the preliminary experiments. In general it was found that sugars and proteins were most suitable, though in addition extracts from natural substances upon which Mycetozoa are frequently found in nature were tried. Finally a series of 10 solutions was selected, which gave a fair range as regards their nutrient qualities.

The solutions finally adopted were, water, glucose 2.0 per cent and 1.0 per cent, starch 1.0 per cent, sucrose 0.3 per cent and 0.15 per cent, peptone 2.0 per cent, Knop's solution and extracts of holly leaves and pea seeds. For use about 50 cc. of the solution were placed in a petri dish about two inches in diameter, into this a sufficient quantity of spores was added to form a more or less even film over the surface, the spores were stirred in for some time in order to get them thoroughly moistened with the solution. With dry spores this wetting of the spore coat is a matter of considerable difficulty, but unless this is done the spores do not germinate. Three series of solutions were set up at the same time except in the case of *Reticularia Lycoperdon* where the rate of germination was very rapid.

Those placed in the light, were put in front of the laboratory window, and a record of the temperature was kept. Those in the dark were placed in a cupboard also in the laboratory and at the same temperature as those in the light. For those which were to be subjected to both darkness and heat an incubator was employed, and the temperature was maintained at 29° C.

Observations were made at frequent intervals, the time depending upon the expected interval before germination. The observations on the spores of *Reticularia* were commenced very soon after the cultures were set up. Since it was impossible to

have all the cultures under observation at the same time an interval of about five minutes at least had to elapse before a culture could be examined for a second time. The records of the times in *Reticularia Lycoperdon* were, therefore, necessarily somewhat inaccurate. In the case of those which took a considerable time to germinate they were examined at intervals of a few hours from the time when, judging from preliminary experiments germination was to be expected. Germination in *Trichia varia* however, was so slow that the observations were made each morning and evening only. Cultures were allowed to run for a considerable time after the first indications of germination in any solution was observed, and if at the end of that time no germination had taken place it was assumed that that solution was unsuitable for spore growth.

In some cases the germination was represented by a percentage. This was taken from several mounts of the spores made by placing a small drop of the solution with the spores in suspension upon the slide and counting those which had germinated and those which had not. Such a method was rough and only represented an approximation of the proportion of the spores which had germinated and were visible in the field. Care, however, was taken not to include in the drop any spores which had not become wetted by the solution. If any were observed in the field, they were neglected; it was found easy to recognise such spores by the shrunken appearance of the spore coat.

RESULTS

The results of the cultures are represented by the following tables, showing the germination and time. In Tables 1, 2, 3 and 5 two distinct series of experiments were made at different times and these can be compared together.

Table 1 shows the germination of *Reticularia Lycoperdon*. It will be seen that germination was obtained in six out of the ten solutions tried; in the case of 0.3 per cent sucrose, germination was obtained in the only instance when it was tried and since successful spore germination was obtained in the weaker solution it is to be expected that the same result would have been obtained in darkness and in dark and heat as was found in light. No

TABLE 1

Reticularia Lycoperdon

Solutions used.	Light.				Dark.				Dark and Heat.			
	Sept. 22		Sept. 29		Sept. 21		Sept. 29		Sept. 21		Sept. 29	
	Germ.	Time.	Germ.	Time.	Germ.	Time.	Germ.	Time.	Germ.	Time.	Germ.	Time.
Water.....	+	82	+	64	+	68	+	68	+	69	+	65
Glucose 1.0%.....	+	65	+	70	+	85	+	85	+	58	+	50
Glucose 2.0%.....	+	80	+	80	+	80	+	95	+	55	+	59
Starch 1.0%.....	+	73	+	58	+	76	+	67	+	48	+	52
Sucrose 0.3%.....			+	80								
Sucrose 0.15%.....	+	75	+	55	+	75	+	60	+	45	+	42
Peptone 2.0%.....												
Holly Extract.....	+	55	+	58	+	52	+	69	+	50	+	48
Pea Extract.....	-		-		-		-		-		-	
Knop's Solution...	-		-		-		-		-		-	

Germination given in approximate percentage. Time given in minutes.
The temperature on Sept. 21, 22 and 29 was 18° C.

germination was found in Pea Extract or in Knop's solution. In peptone the formation of bacteria made the estimation of the percentage germination difficult to determine, though there is no doubt that some of the spores liberated their contents within an hour. The temperature of the light culture was 18° C. and those in darkness were maintained at the same temperature.

The spores which were sown on Sept. 22 were obtained from near Sevenoaks, Kent, the previous June; those used on Sept. 29 were from an old stock which had also been collected near Sevenoaks; the date of this collection is not known but they were at least five years old. It is very interesting to note that there was no loss in the vitality of the spores even after five years. This is in accordance with previously observed data, several old collections of the spores of *Reticularia Lycoperdon* have been kept in the Department and they appear to keep their vitality up to about seven years after collecting.

The differences in the rate of germination in the three types of physiological conditions are insufficient to justify any definite conclusions being drawn from them. On the whole the rate seems to be slightly accelerated by heat, but the difference in time

TABLE 2
Stemonitis splendens var. *flaccida*

Solutions used.	Light.				Dark.				Dark and Heat.			
	Sept. 11		Sept. 15		Sept. 11		Sept. 15		Sept. 11		Sept. 15	
	Germ.	Time.	Germ.	Time.	Germ.	Time.	Germ.	Time.	Germ.	Time.	Germ.	Time.
Water.....	—	—	1	21	—	—	5	26	—	—	2	21
Glucose 1.0%.....	1	21	10	26	5	27	15	26	—	—	—	—
Glucose 2.0%.....	—	—	10	26	50	27	50	26	—	—	10	26
Starch 1.0%.....	5	27	1	26	5	21	—	—	15	27	10	26
Sucrose 0.3%.....	—	—	—	—	—	—	—	—	—	—	—	—
Sucrose 0.15%.....	—	—	—	—	20	21	2	20	4	27	1	26
Peptone 2.0%.....	20	20	*	—	60	26	*	—	—	—	*	—
Holly Extract.....	—	—	50	21	—	—	50	21	—	—	25	21
Pea Extract.....	—	—	25	21	—	—	10	21	—	—	10	21
Knop's Solution...	15	20	10	20	30	21	5	21	2	27	—	—

Germination given in approximate percentage. Time given in hours.

The temperature on Sept. 11, was 17° C. and on Sept. 15, 18° C.

Contaminated with bacteria.

is insufficient to be of fundamental importance. The most rapid germination was in dilute sucrose solution, where it took place in 42 minutes.

Table 2 shows the results obtained with *Stemonitis splendens* var. *flaccida*. These spores germinated very much more slowly than those of *Reticularia Lycoperdon*. It was also found possible to give the germination as a percentage. The result on the two occasions when the spores were sown is variable but in general it shows that the best results can be obtained with 2.0 per cent glucose, 1.0 per cent starch and with 0.15 per cent sucrose, it is interesting to note that no germination was obtained with the stronger solution of sucrose. Knop's solution gave satisfactory results except in the dark and heat. Extracts of pea and holly proved to be very suitable as was to be expected from the habitat where this species is to be found. The result with 2.0 per cent peptone was interesting, in both light and darkness good germination was generally obtained, but under the influence of heat no swarm spores were obtained. In the second attempt the formation of bacteria in this solution prevented any observations being made. The general inference from this table is that the spores of *Stemonitis splendens* var. *flaccida* germinate better in the dark

TABLE 3
Fuligo septica

Solutions used.	Light.				Dark.				Dark and Heat.			
	Sept. 14		Sept. 15		Sept. 14		Sept. 15		Sept. 14		Sept. 15	
	Germ.	Time.	Germ.	Time.	Germ.	Time.	Germ.	Time.	Germ.	Time.	Germ.	Time.
Water	—		—		—		—		—		+	23
Glucose 1.0%	—		+	24	—		+	25	+	24	+	25
Glucose 2.0%	—		+	24	—		+	24	+	24	—	
Starch 1.0%	—		—		—		—		—		—	
Sucrose 0.3%	—		—		—		—		—		—	
Sucrose 0.15%	—		—		—		—		—		—	
Peptone 2.0%	—		—		—		—		—		—	
Holly Extract	—		—		—		—		—		—	
Pea Extract	—		—		—		—		—		—	
Knop's Solution	—		—		—		—		—		—	

Germination given without percentage, but in no case did it exceed 10 per cent of the spores examined. Time given in hours.

The temperature on both Sept. 14 and 15 was 18° C.

than in the light and that the effect of heat is to decrease the rate of germination in all solutions except starch.

The sporangia used in these two cases were obtained from different parts of Epping Forest during the autumn of 1927.

Table 3 shows the germination of *Fuligo septica*. It was very much more difficult to obtain any definite results with these spores. The best was with 1.0 per cent glucose, where germination occurred in all three conditions, and in one instance on both occasions when germination was tried. With 2.0 per cent glucose the same result was obtained once in the light, once in the dark and once in darkness and heat. In one case it was obtained in water, in darkness and heat. No other solution gave any positive results at all. *Fuligo septica* grows chiefly on rotten wood and it is remarkable that no swarm spores were found in extracts of natural substances. The spores used in these experiments were collected from diverse localities, those used on Sept. 14 from Oxshott, Surrey, those on Sept. 15 from near Bournemouth, Hampshire.

Table 4 shows the germination of *Lycogola epidendrum*. Although this species grows and fruits generally throughout the

TABLE 4

Lycogola epidendrum

	Light.		Heat.		Heat and Light.	
	Sept. 23		Sept. 23		Sept. 23	
	Germ.	Time.	Germ.	Time.	Germ.	Time.
Water.....	2	68	4	72	—	
Glucose 1.0%.....	15	68	70	68	—	
Glucose 2.0%.....	10	69	10	69	—	
Starch 1.0%.....	15	69	8	69	3	69
Sucrose 0.3%.....	—		—		—	
Sucrose 0.15%.....	8	71	35	71	—	
Peptone 2.0%.....	—		—		—	
Holly Extract.....	—		50	71	—	
Pea Extract.....	—		—		—	
Knop's solution.....	—		—		—	

Germination given in approximate percentage. Time in hours. The temperature was 18° C.

year, scarcely any swarm spores were produced in the heat, though in glucose, starch and sucrose fair germination was found in both light and darkness. No swarm spores were found in Knop solution or in 0.3 per cent sucrose. The germination in tap water was not so good as in the other solutions. The time taken for any swarm spores to appear was considerably longer than in any of the species already considered, but the percentage germination was quite good. The material was collected from Oxshott, Surrey in July 1927, and the results are in agreement with the preliminary observations made.

Table 5 gives the results of the germination of *Trichia varia*. It is generally found very difficult to obtain swarm spores from any species of this genus. This may in part be due to the time which must elapse between the sowing of the spores and the appearance of the swarm spores. It was not found possible to examine the cultures sufficiently often to give the times of germination in hours and they are therefore represented in days. The most rapid germination was five days. Germination was most successful in 1.0 per cent starch, with this swarm spores were obtained on all occasions. There was a general tendency for less germination in heat than in the colder conditions. Those grown in light on Jan. 11 were placed in an unheated greenhouse,

TABLE 5

Trichia varia

Solutions Used.	Light.				Dark.				Dark and Heat.			
	Dec. 14.		Jan. 11		Dec. 14		Jan. 11		Dec. 14		Jan. 11	
	Germ.	Time.	Germ.	Time.	Germ.	Time.	Germ.	Time.	Germ.	Time.	Germ.	Time.
Water.....	2	7	2	6	1	6	5	6	—	—	—	—
Glucose 2.0%.....	1	7	4	6	3	6	1	5	3	6	—	—
Glucose 1.0%.....	2	7	1	5	25	5	1	6	1	6	—	—
Starch 1.0%.....	2	7	5	5	2	6	1	5	2	6	2	6
Sucrose 0.3%.....	—	—	1	6	—	—	—	—	—	—	—	—
Sucrose 0.15%.....	—	—	—	—	—	—	—	—	1	6	—	—
Peptone 2.0%.....	—	—	—	—	1	6	—	—	1	6	—	—
Holly Extract.....	—	—	1	6	2	5	—	—	—	—	—	—
Pea Extract.....	—	—	—	—	—	—	—	—	—	—	—	—
Knop's Solution...	—	—	2	6	1	5	1	5	—	—	—	—

Germination given in approximate percentage. Time given in days. The temperature on Dec. 14 varied considerably, being as low as -2°C . on at least one occasion, that on Jan. 11 was 18°C .

and it is known that one night the temperature fell to 30°F ., yet the difference in the rate of germination from that on Dec. 14 when the cultures were set up in the laboratory at 18°C . was not very noticeable, in general there appeared to be a slight slowing off of the rate, though germination occurred in some cultures only at the lower temperature. *Trichia varia* is a common winter species and it was to be expected that a low temperature would not impede germination. 25 per cent germination in glucose on Dec. 14 was not in accordance with what was found in any of the other cultures and stands apart as a much better proportion of viable swarm spores than anywhere else, that this could not be repeated suggests that these spores were in some way different from the rest, although they were obtained from the same mass of sporangia as the others. All the spores used were collected in Epping Forest during October 1927.

From these five tables it can be seen that the spores of very diverse types of Mycetozoa are capable of being germinated in artificial solutions with comparative certainty though the quantity of germination will vary within wide limits. The time taken for germination varies very much in the different genera though

in general species of the same genus germinate in approximately the same time in the same solution. The growth in light, darkness and heat seems to affect species in different ways though in general heat is not advantageous to growth of the swarm spores. Light is of advantage to some while darkness benefits others, the habitat on which they live in nature does not seem to influence these results.

Attempts were made to try and grow some of these forms on agar plates, but, although they germinated readily in solutions, no positive results were obtained with agar. This is probably at any rate partly due to the comparative dryness of the agar plates and also to the facility with which other fungal spores start to grow and soon cover the plates. No satisfactory way of preventing the appearance of these fungi was found. The addition of acid or alkalis to the medium was thought to have a deleterious effect upon the swarm spores and was not adopted.

DISCUSSION

Comparatively little has been published on the germination of Mycetozoa under artificial conditions. In 1894 Durand (3) studied the germination of *Enteridium Rozeanum*. He found that the spores required a period of rest before germination would take place. The best temperature to obtain a large proportion of swarm spores he concluded was about 28° C. We found that satisfactory germination was obtainable at about 18° C. Durand observed that in some cases swarm spores were produced having a flagellum at each end.

Previously de Bary (1) had succeeded in germinating the spores of *Fuligo septica* and *Trichia varia*, and observed that occasionally swarm spores with two flagella were produced, though in this case, it is doubtful whether both were formed at the same end.

In 1893 McClatchie (6) reported the germination of the spores of *Reticularia Lycoperdon*. He found that no period of rest was required, and that it was possible to induce the formation of swarm spores within an hour after placing them in distilled water. He also succeeded in germinating the spores of *Diachaea leucopoda*, *Hemitrichia Vesparium*, *Fuligo septica* and *Badhamia capsulifera*; only a small proportion of these produced swarm spores, and he

concluded that this was due to the fact that the collections were two months old.

Miller (7) in 1899 carried out further experiments on the germination of Mycetozoa spores under aseptic conditions. He cultivated these in flasks using infusions of hay. In some cases he was able to obtain not only plasmodia but also fructifications in his cultures.

In 1906 Constantineanu (2) published his important contribution to the subject. He studied the germination of a large number of species both in organic and in inorganic substances, and endeavoured to discover what substances were made use of by the swarm spore during its growth. It is interesting to compare the time taken for germination in the species he examined with our own. In distilled water he found that the rate of germination varied from 30 minutes in *Reticularia Lycoperdon* to 24 hours in *Physarum didermoides*, though in the latter species he admits that sometimes they took as long as two or three days, or in a few cases even longer. He tried the effect of carbohydrates, but came to the conclusion that these alone were insufficient to give good results; he found that sucrose was better than glucose. He also made experiments with natural substances, such as extracts of bark, branches and seeds, he found that these were very suitable for the germination of all species of Mycetozoa. He also went on to study the growth of the plasmodia in various media.

In general, his results are in agreement with our own. In *Reticularia Lycoperdon* he obtained germination in 30 minutes in water, while we found that it took from 64 to 82 minutes, but he found that in order to obtain a 50 per cent formation of swarm spores the time required was from 2 to 3 hours, while in the present instance a 50 per cent germination was obtainable in little over an hour. McClatchie also found that the swarm spores of this species appeared in about an hour after sowing.

In *Stemonitis splendens* var. *flaccida* he obtained germination in from 5 to 6 hours; in the present case the time was considerably longer, from about 21 hours. To get a 25 per cent germination took up to from 12 to 48 hours, whereas we found in a solution of peptone a 60 per cent germination in 26 hours, and in extracts of Holly in 21 hours.

Fuligo septica we found very difficult to germinate at all, Constantineanu found swarm spores in from 30 minutes to 90 minutes. We found no germination in water, except in heat and darkness; germination was best in glucose solutions.

Lycogola epidendrum he germinated in 60 hours in water; those we tried took from 68 to 72 hours, though the percentage of germination was much lower. Only in Holly extract did the percentage germination reach anything comparable with what Constantineanu obtained.

He found that *Arcyria denudata* germinated in about 9 hours, while we found that in the related genus *Trichia*, *T. varia* required as much as five days.

In most cultures the swarm spores appeared to be quite normal; they remained active for a varying period, sometimes becoming amoeboid, and then regaining their flagellated condition. Some of the cultures were kept for several days, but in no case did any indications of the formation of a plasmodium appear. It is probable that they required some substratum on which to grow, and failing this they were incapable of further life. It has been observed that plasmodia of various species can be produced in agar cultures, particularly when grown in tubes, in this case the plasmodium generally migrates from the surface of the agar and swarms up the surface of the glass.

In 1907 Pinoy (8) suggested that bacteria played a part in the germination of the spores of all Mycetozoa. Although in the older cultures these are almost invariably present, yet in species like *Reticularia Lycoperdon* where germination is rapid no bacteria could be detected at the time when the swarm spores appeared, though later the cultures became contaminated with them.

Since the appearance of Constantineanu's paper little has been published on the subject, though a few workers have obtained plasmodia artificially for various purposes. In 1927 Gilbert (4) suggested that those bodies appearing in cultures of swarm spores possessing more than one flagellum were foreign bodies. He found both in *Hemitrichia clavata* and in *Stemonitis fusca* organisms having either a flagellum at each end or two at the anterior. He considered that these were Protozoa, and referred them to the genus *Cercomonas*, as *Cercomonas longicauda*. In our cultures of

Stemonitis splendens var. *flaccida* we have observed forms with as many as three flagella. Though they appear sparingly in some culture solutions they are entirely absent in others. No multi-flagellated swarm spores were found in any of the other species examined.

Multiflagellated swarm spores have been sometimes observed in cultures of a number of species, and it seems unlikely that these are all due to the presence of a Protozoan invader. It is not unreasonable to assume that under certain abnormal nutrient conditions swarm spores with more than a single flagellum can be produced.

SUMMARY

1. Spores of several species of Mycetozoa including *Reticularia Lycoperdon*, *Fuligo spetica*, *Stemonitis splendens* var. *flaccida*, *Lycogola epidendrum* and *Trichia varia*, have been successfully germinated in artificial solutions.

2. The rate of germination varied in the different species; *Reticularia Lycoperdon* taking about an hour, *Trichia varia* about five days.

3. Tables are given showing the proportion of germination and the time taken, in respect to a number of organic substances. The effect of light, darkness and combined darkness and heat was tried. The results differ in the various species and no general conclusions could be arrived at.

4. Evidence is brought forward to show that the length of time taken by the spores of a species collected from different localities to germinate does not differ appreciably, no more than do the spores of the same mass of sporangia when grown at different times under the same conditions. It has been found that the spores of *Reticularia Lycoperdon* do not lose their vitality in five years, though after seven years germination is uncertain. The same vitality is not shown by other species, *Trichia varia* losing its power of germination in about a year.

Our thanks are due to Professor R. R. Gates for reading through the proofs and for helpful criticisms during the work.

KING'S COLLEGE,
UNIVERSITY OF LONDON,
February, 1928.

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NOTES AND BRIEF ARTICLES

A Correction

In the May-June issue of MYCOLOGIA, 1928, volume 20, number 3, page 153, was published a description of a new genus of fungi. Line 13 from the top of page 153, reading "*Monilinia fructicola* (Winter) comb. nov." should be deleted. EDWIN E. HONEY.

ROMUALDO GONZALEZ FRAGOSO

+ JUNE 3, 1928

With the death of Doctor Romualdo González Frago, chief of the Cryptogamic Laboratory of the Real Jardín Botánico de Madrid, Spanish mycology has lost its most distinguished scholar. In a short period of time, the Spanish-speaking world has lost its two most eminent mycologists: the well-known Doctor Carlos Spegazzini, an Italian by birth, and Professor Gonzalez Frago.

The work he leaves behind is of the greatest importance, especially along the lines of systematic mycology. Our present knowledge of the fungous flora of Spain and Portugal should justly be credited, almost exclusively, to his tireless efforts. In late years he realized the convenience of bringing together in monographic form his numerous works on the flora of the Iberian peninsula and had already published two volumes on the Uredinales, one on the Hyphales and a complete census of the other Deuteromycetes, exclusive of the Sphaeropsidales, and also of the Ustilaginales. He has also published contributions on the fungi of Morocco, Mexico and Santo Domingo. Of this latter country, he was making an extensive study, and had published, in collaboration, fifteen serial contributions. His untimely death came just as he was completing his sixteenth series.

CARLOS E. CHARDON AND R. CIFERRI.

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